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Research Document 2011/037

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Document de recherche 2011/037

Région de la Capitale Nationale et région du Golfe

La mauvaise condition des poissons peut-elle expliquer la mortalité naturelle élevée chez la morue et chez d'autres poissons marins dans le sud du golfe du Saint-Laurent?

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Ce document est disponible sur l'Internet à:

ISSN 1499-3848 (Printed / Imprimé)
ISSN 1919-5044 (Online / En ligne)
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Canada

Correct citation for this publication:

Swain, D.P., H.P. Benoît, L. Savoie, and T. Surette. 2011. Can poor fish condition explain the elevated natural mortality of cod and other marine fish in the southern Gulf of St. Lawrence? DFO Can. Sci. Advis. Sec. Res. Doc. 2011/037. iv + 26 p.

ABSTRACT

Natural mortality (M) of older (5+ yr) southern Gulf of St. Lawrence cod has been elevated throughout the 1990s and 2000s. In the northern Gulf cod population, increased natural mortality has been hypothesized to reflect increased starvation due to poor fish condition, resulting from harsh (cold) environmental conditions. We examined whether poor condition may explain the elevated natural mortality of cod and other marine fish in the southern Gulf. Temperature of the Cold Intermediate water Layer (CIL) in the Gulf of St. Lawrence was below normal in the early to mid 1990s, but then increased and has been above average throughout the 2000s. There has been no decrease in M of 5+ southern Gulf cod in response to the warming of the CIL. In contrast to CIL temperature, the ambient temperature of cod (i.e., bottom water temperature in the areas occupied by cod) in September during the feeding season was near average levels throughout the 1990s and 2000s. Ambient temperature of southern Gulf cod was lowest in the early to mid 1980s, when M of 5+ cod was estimated to be substantially lower than in the 1990s and 2000s. Cod in the southern Gulf exhibit a marked seasonal cycle in condition, with lowest condition in the spring. Southern Gulf cod are in better condition in the spring than reported for the northern Gulf stock. It has been suggested that cod are at increased risk of mortality when their condition factor K is less than 0.7. In the early 1990s, the proportion of cod with $K < 0.7$ was much lower in the southern Gulf stock than observed in the northern Gulf stock. This proportion has since dropped to even lower levels. Overwinter mortality of fish in poor condition could result in a truncation in the distribution of K at low values. There is no indication of such truncation in the distribution of cod condition in spring. Condition of southern Gulf cod in spring improved substantially from the 1990s to the 2000s, but this was not reflected in any decline in M . Over the longer 1971-2009 period, the strongest changes in condition occurred in the late 1970s and early 1980s. Condition in September was at the lowest levels observed in this 40-yr period in the early to mid 1980s. Estimated 5+ M was substantially lower then than in the 1990s and 2000s. At the community level, there is no association between patterns in condition and trends in abundance or mortality. Some species with elevated natural mortality show little seasonal variation in condition (e.g., winter skate); others with strong seasonal cycles in condition do not appear to have elevated natural mortality (e.g., Greenland halibut, herring). Similar interannual patterns in condition are shared between species that have declined in abundance and have elevated mortality and those with stable abundance. For species with estimated trends in M , periods of low condition are generally not coincident with periods of increasing or high M . Increased starvation due to poor condition does not appear to be an important cause of the current high levels of M for 5+ cod and other large demersal fish in the southern Gulf of St. Lawrence.

RÉSUMÉ

La mortalité naturelle (M) chez les morues plus âgées (5 ans ou plus) dans le sud du golfe du Saint Laurent était élevée dans les années 1990 et 2000. Pour la population de morues du nord du golfe, on supposait que la mortalité naturelle élevée résultait de l'augmentation de la famine due à la mauvaise condition des poissons, celle-ci étant causée par les conditions environnementales difficiles (froid). Nous avons voulu savoir si la mauvaise condition des poissons pouvait expliquer la mortalité naturelle élevée chez les morues et chez d'autres poissons de mer dans le sud du golfe du Saint-Laurent. La température de l'eau de la couche intermédiaire froide (CIF) dans le golfe du Saint-Laurent était inférieure à la normale au début et au milieu des années 1990, mais a de nouveau augmenté et dépassé la moyenne dans les années 2000. La M des morues de 5 ans et plus dans le sud du golfe n'a pas diminué avec le réchauffement de la CIF. Contrairement à la température de la CIF, la température ambiante de la morue (c.-à-d. la température de l'eau de fond des zones occupées par les morues) au mois de septembre pendant la période d'alimentation était proche de la moyenne dans les années 1990 et 2000. La température ambiante des morues du sud du golfe du Saint-Laurent était plus basse au début et au milieu des années 1980, période où l'on estimait que la M chez les morues de 5 ans ou + était considérablement plus basse que dans les années 1990 et 2000. La morue du sud du golfe du Saint-Laurent présente une condition marquée par un cycle saisonnier qui est au niveau le plus bas au printemps. La morue du sud du golfe du Saint-Laurent est en meilleur état au printemps que la morue du nord du golfe. Il a été suggéré que les morues connaissent un risque élevé de mortalité lorsque leur coefficient de condition K est inférieur à 0,7. Au début des années 1990, le nombre de morues présentant un K inférieur à 0,7 était inférieur dans les stocks du sud du golfe du Saint-Laurent que dans ceux du nord du golfe. Depuis ce temps, cette proportion a atteint des niveaux encore plus bas. La mortalité chez les poissons en mauvaise condition pendant l'hiver pourrait entraîner une troncation de la répartition du K à faibles valeurs. Rien n'indique une telle troncation de la répartition de la condition de la morue au printemps. La condition des morues du sud du golfe du Saint-Laurent au printemps s'est considérablement améliorée des années 1990 aux années 2000, mais cette tendance n'était pas accompagnée d'une baisse de la M . Au cours de la période plus longue allant de 1971 à 2009, les changements les plus importants de la condition des morues ont eu lieu à la fin des années 1970 et au début des années 1980. La condition des morues au mois de septembre était à son niveau le plus bas enregistré au cours de cette période de 40 ans au début et au milieu des années 1980. La M estimée des morues de 5 ans ou plus dans cette période de mauvaise condition était considérablement plus basse que dans les années 1990 et 2000. Au niveau de la communauté, aucun lien n'est établi entre les variations de la condition des morues et les tendances en matière d'abondance ou de mortalité. Certaines espèces à la mortalité naturelle élevée présentent une faible variation saisonnière de leur condition (p. ex., raie tachetée); d'autres, connaissant de forts cycles saisonniers de leur condition, ne semblent pas présenter de mortalité naturelle élevée (p. ex., flétan du Groenland, hareng). Des tendances interannuelles similaires de la condition se retrouvent chez les espèces dont l'abondance a diminué et la mortalité a augmenté, et celles dont l'abondance est demeurée stable. Pour les espèces dont les tendances de la M sont estimées, des périodes de mauvaise condition ne coïncident en général pas avec des périodes de M élevée. La famine accrue due à une mauvaise condition ne semble pas être un facteur important du niveau actuel élevé de la M chez les morues de 5 ans ou plus et chez d'autres poissons de fond du sud du golfe du Saint-Laurent.

INTRODUCTION

Cod in the northern and southern Gulf of St. Lawrence populations have a strong seasonal cycle in condition (Lambert and Dutil 1997; Schwalme and Chouinard 1999). Condition of these fish is at its lowest level in the spring, following the overwintering period when little feeding occurs. Condition of some individuals is sufficiently low in spring (e.g., condition factor < 0.7) that they are thought to be at increased risk of mortality due to starvation and energetic depletion (Lambert and Dutil 1997; Schwalme and Chouinard 1999).

Natural mortality appeared to be at an elevated level in the mid to late 1990s in many Northwest Atlantic cod stocks (e.g., Shelton et al. 2006). One hypothesis proposed to account for this observation is that natural mortality increased in the early 1990s due to poor fish condition, resulting from harsh (cold) environmental conditions (Lambert and Dutil 1997, Dutil et al. 1999, Dutil and Lambert 2000). This hypothesis was developed based on data for the northern Gulf of St. Lawrence (nGSL) cod stock. The Cold Intermediate Layer (CIL), which comprises the bottom waters in shelf areas of the Gulf, cooled in the 1980s, resulting in a period of cold temperatures in the early to mid 1990s (e.g., Gilbert and Pettigrew 1997; Fig. 1). Lambert and Dutil (1997) noted that declines in the condition of northern Gulf cod coincided with the onset of this cold period. Condition of nGSL cod in January declined in the late 1980s and early 1990s. Seasonal sampling between June 1993 and June 1995 revealed that condition reached a very low level in May 1994, when the mean condition factor (Fulton's K) was 0.69 and 75% of fish had K less than 0.7. The distribution of K in these fish overlapped slightly with the distribution in starved fish that died or became moribund in laboratory experiments, though the majority of starved fish had considerably lower values (<0.5). Dutil and Lambert (2000) compared condition indices of these wild northern Gulf cod with those of dead starved cod, surviving starved cod and fed cod from laboratory experiments. While few (0.4%) of these wild cod had characteristics similar to those of laboratory deceased cod, substantial proportions (18-66%) had characteristics more similar to those of starved cod than fed controls. These observations led to the conclusion that the energy reserves of nGSL cod were severely depleted in spring (April-June) in the early 1990s, possibly leading to increases in natural mortality in these fish.

In this paper, we examine whether poor fish condition may be an important factor in the elevated natural mortality (*M*) of southern Gulf of St. Lawrence (sGSL) cod in the 1990s and 2000s. We also examine trends in condition in the sGSL fish community to determine whether patterns in condition are congruent with community-wide patterns in mortality (Benoît and Swain, 2011).

TRENDS IN ENVIRONMENTAL TEMPERATURE VERSUS AMBIENT TEMPERATURE OF COD

The forcing factor proposed to underlie the poor condition of nGSL cod in the early to mid 1990s was temperature, with poor condition resulting from the prolonged period of cold CIL waters in the early to mid 1990s. In this section, we describe interannual variation in CIL temperature in the sGSL, and contrast the pattern in CIL temperature with variation in the ambient temperature of sGSL cod. Ambient temperature is defined here as the near-bottom water temperature in the areas occupied by cod.

Figure 1 shows an index of CIL temperature in the sGSL, based on temperatures in the 60-120 m water layer in September. CIL temperature was relatively warm in the late 1970s and early

1980s but then declined, with a period of below average CIL temperature extending from the late 1980s to the late 1990s. Temperature then warmed, with above average CIL temperatures in 9 of the 11 years since 1999. If poor condition due to cold temperatures were an important cause of the elevated M of sGSL cod in the 1990s, a decline in M to normal levels in the 2000s would be expected (unless some other factor replaced cold temperature as a cause of high M). In contrast to this expectation, estimated M did not decline in the 2000s (Swain 2011a,b).

It might be argued that condition of cod should be more closely linked to variation in the ambient temperature of cod than to variation in a general index of temperature conditions. Figure 2 shows indices of the ambient temperature of sGSL cod in September, during the feeding season. This index is based on bottom temperature measurements and cod catches in the annual September bottom-trawl survey, and is calculated as follows (Perry and Smith 1994):

$$T_c = \sum_{i=1}^N w_i T_i c_i / \bar{C}$$

where w_i is the weight associated with tow i , T_i is the bottom temperature for tow i , c_i is the cod catch in tow i and \bar{C} is the stratified mean cod catch in the survey. The weighting factor w_i is the proportion of the survey area covered by the stratum in which tow i was made divided by the number of tows made in that stratum.

The time trend in the ambient temperature of cod differs markedly from the trend in the CIL index (Figures 1 and 2). In contrast to CIL temperature, the ambient temperature of cod was warmest in the mid 1970s and coldest in the early to mid 1980s. Ambient temperature was near the long-term average throughout the 1990s and in the 2000s. The difference between the trends in CIL temperature and cod ambient temperature reflects density-dependent shifts in cod distribution (Swain 1993; Swain and Kramer 1995; Swain 1999). Cod distribution during the feeding season in September shifted offshore into colder water when abundance increased in the late 1970s and early 1980s and back into warmer shallower water when abundance declined in the 1990s. Thus, in contrast to CIL temperature, ambient temperature of cod during the feeding season was not unusually low during the 1990s; instead, it was near the long-term average.

CONDITION AND NATURAL MORTALITY OF COD

EVIDENCE FROM SEASONAL MONITORING OF CONDITION

Methods

Seasonal condition of sGSL cod has been monitored since September 1991. Sampling has followed the seasonal distribution of sGSL cod. Sampling in winter has been in the 4Vn area where the stock overwinters. Early spring samples were taken off northwestern Cape Breton along the migration route into the Gulf. Later in the spring and early summer, samples were taken in the western Gulf where the main spawning grounds occur. During the feeding season in late summer and early fall, samples were taken throughout the Gulf during synoptic bottom-trawl surveys. In late fall, samples were again taken off northwestern Cape Breton along the migration route out of the Gulf.

Length-stratified samples were obtained so that size distribution was similar between samples. The target was 5 fish per 1-cm length interval between 35 and 60 cm, plus a random sample of up to 50 fish <35 cm and 50 fish >60 cm. Fish < 35 cm or greater than 65 cm in length were excluded from the analyses reported here. Measurements taken on each fish included fork length, total weight, and weights of the liver, gonad and stomach. Measurements on 20,968 fish were examined.

More intensive sampling was conducted in the spring in 2009 (April 30 – May 3) and 2010 (April 21 – 22) to better characterize the distribution of condition at this time of year when condition is at its lowest. A survey consisting of 20 bottom-trawl tows was conducted in the Cape Breton Trough and along the south slope of the Laurentian Channel between Cape Breton and the Magdalen Islands, the routes used by cod as they migrate into the Gulf in spring. Sample sizes were 774 in 2009 and 644 in 2010.

Two indices of condition were calculated:

1) Fulton's $K = 100 * W/L^3$, where L is fork length (cm) and W is somatic weight (g). Somatic weight is total weight minus the weights of the gonads and the stomach and its contents.

2) Hepatosomatic index, HSI = liver weight expressed as a percentage of somatic weight.

We modelled the seasonal cycle in condition (K and HSI) as follows. Temporal variation in cod condition indices can be modelled with a periodic annual component whose particular characteristics also follow inter-annual trends. We constructed a spline model with both periodic (seasonal) and global (interannual) trend components. Within a given year, the periodic component was assumed to vary smoothly down to a minimum (spring) and then increase to a maximum (fall). Let the times at which these extremes occur be labelled t_{\min} and t_{\max} . These

serve as knots in the periodic spline, and are parameters to be estimated. Let $f(t) = \sum_{j=0}^5 a_j t^j$ be

a 5th-order polynomial serving as the basic function for the periodic component of the spline model. Now suppose we have two polynomials $f_0(t)$ and $f_1(t)$ and join them using the following continuity and smoothness constraints:

$$\begin{array}{ll} f_0(t_{\min}) = f_1(t_{\min}) = h_{\min} & f_0(t_{\max}) = f_1(t_{\max}) = h_{\max} \\ f_0'(t_{\min}) = f_1'(t_{\min}) = 0 & f_0'(t_{\max}) = f_1'(t_{\max}) = 0 \\ f_0''(t_{\min}) = f_1''(t_{\min}) = h_{\min}'' & f_0''(t_{\max}) = f_1''(t_{\max}) = h_{\max}'' \end{array}$$

Note that the zero constraint on the first derivative implies that an extrema lies at the knots t_{\min} and t_{\max} . The minimum and maximum condition indices at these knots are thus h_{\min} and h_{\max} , respectively. Under these constraints a unique solution of the polynomial coefficients a_0, \dots, a_5 exists for each of the two interpolating polynomials (one for the ascending limb of the seasonal cycle and one for the descending limb). To account for interannual trends, some of the periodic spline parameters, namely the minimum and maximum condition indices h_{\min} and h_{\max} , were defined to vary as functions of time, $h_{\min}(t)$ and $h_{\max}(t)$. For convenience, these were also

specified as 5th-order polynomials. The model was fit numerically via maximum likelihood assuming normally-distributed errors.

Condition of nGSL cod is at its lowest level in April – June (Dutil and Lambert 2000). We examined interannual variation in condition of sGSL cod during this period using the following model:

$$h_{ij} = \beta_{0i} + \beta_1 d_{ij} + \varepsilon_{ij}$$

where h_{ij} is condition of the j^{th} fish caught on calendar day d_{ij} in year i , ε_{ij} is a normally distributed random deviate with mean 0, and β_{0i} and β_1 are parameters to be estimated.

A model with heterogeneous slope was also examined, though some years had to be grouped together (1997 and 2000, 2003 and 2004) to obtain reliable parameter estimates with the heterogeneous slope model. Examination of residuals indicated that a linear model provided an adequate fit to the data.

The distribution of condition in samples collected in April and early May was examined for evidence of truncation at lower values of condition, as would be expected if fish with low condition had been lost to mortality.

Results

Cod in the sGSL are in better condition in spring than has been observed in the nGSL (Fig. 3). No samples from the sGSL showed condition levels as poor as observed in the May 1994 sample from the nGSL, and only one sample (May 1992) resembled the less severe condition levels observed in the nGSL in May 1995. The percent of nGSL cod with $K < 0.7$ was 75% in May 1994 and 43% in May 1995. The percent of sGSL cod with $K < 0.7$ was 35% in early May 1992, about 20% in late April 1993 and 2001, and less than 10% in late April and early May samples in other years (mean=5%).

Figures 4 and 5 show mean condition factor K and HSI in seasonal samples of sGSL cod from September 1991 to July 2010. Condition in spring was higher in the 2000s than in the 1990s. This is most evident for K , which decreased to lower values in spring in the 1990s than in the 2000s. Minimum values of HSI changed little over the time series, but HSI increased more rapidly in spring in the 2000s than in the 1990s.

A seasonal condition model which allowed for interannual variation in minimum and maximum condition fit the data much better than a model with constant minima and maxima ($P < 0.0001$, Fig. 6). This model indicated that seasonal minimum values of K were higher in the 2000s than in the 1990s. The model fit to HSI indicated less interannual variation in seasonal minimum values of HSI (Fig. 7).

For both K and HSI, all terms were highly significant ($P < 0.0001$) in the model relating condition in April – June to year and calendar day. The interaction term (year x slope) was significant, but it was relatively unimportant compared to the main effects. For K , model R^2 was 0.393, with year accounting for 20.5% of the sums of squares, calendar day accounting for 16.1%, and their interaction accounting for 2.7%. For HSI, model R^2 was 0.431, with year accounting for 8.2% of the sums of squares, calendar day accounting for 31.4%, and their interaction accounting for 3.5%. Residual plots indicated that a linear model for the effect of day provided an adequate fit

to the data (Fig. 8). Results for predicted condition on May 23 (the mean date in the April-June data) were similar between models with and without an interaction (i.e., assuming homogeneous versus heterogeneous slopes), except that predicted condition in the grouped 1998 and 2000 data was unusually low in the model with an interaction term (Fig. 9). This likely reflected a biased estimate of the slope for the data grouped over these two years. Only a narrow range of days was available for these years, so the estimate for the slope was inflated by the interannual difference in condition between samples. Predicted condition on May 23 was quite variable in the 1990s, with relatively low values for 1992, 1994 and 1998 and a relatively high value for 1993. Predicted condition has been at a relatively high level since the early 2000s.

If substantial numbers of fish with $K < 0.7$ were suffering condition-dependent overwinter mortality, the distribution of K would be expected to be truncated at low values in the spring. The distributions of K in spring samples of sGSL cod do not show evidence of truncation at low values (Fig. 10).

Discussion

One hypothesis for a cause of the elevated natural mortality of cod is that it is due to increased starvation mortality due to poor condition in spring. Harsh (cold) environmental conditions are hypothesized to result in poor condition of cod. Environmental conditions in the Gulf of St. Lawrence were cold in the early to mid 1990s, but warmed in the late 1990s to average or above-average levels. Thus, the current high levels of natural mortality (M) of sGSL cod cannot be attributed to cold conditions. Prey of cod are currently at a high level of abundance in the sGSL (Benoît and Swain 2008; H.P. Benoît, unpublished analyses), and cod abundance is low, so feeding opportunities for cod are good, and elevated mortality due to poor fish condition would not be expected in this population in the 2000s.

Condition of sGSL cod in the spring has been at a relatively high level since the early 2000s. Despite this increase in condition, there has been no decline in M . This is inconsistent with the hypothesis that starvation due to poor condition is an important cause of elevated M in this stock, at least in the 2000s.

Condition of sGSL cod in the spring was lower in the 1990s, in particular in 1992. However, even then, spring condition in this stock was considerably better than that observed in the nGSL stock in the early to mid 1990s. Because seasonal monitoring began in the fall of 1991, it is not known whether spring condition in the early 1990s was unusually low, perhaps contributing to the increased M observed then, or similar to that observed in earlier years when M was lower. No truncation of the distribution of condition at low values, symptomatic of the loss of these fish to natural mortality, was evident even in the 1990s samples. If condition is hypothesized to have been unusually low in the 1990s, the forcing factor is unclear. Although CIL temperature was low then, the temperatures actually occupied by cod during the feeding season were near the long-term average for this stock.

LONG-TERM TREND IN CONDITION OF COD

A longer term perspective on variation in the condition of sGSL cod is available from length-weight data collected during the annual September bottom-trawl survey (Fig. 11). Condition of cod in September was high in the early to mid 1970s, declined to the lowest levels observed in the 40-yr record in the late 1970s to mid 1980s, and then increased to levels near the long-term average throughout the 1990s and 2000s. This variation in condition showed a weak positive

relationship with the ambient temperature of cod during the feeding season and a strong negative relationship with cod density (see below). The low condition in the late 1970s to mid 1980s was associated with unusually strong yearclasses of cod and a shift in distribution into colder water.

This longer term data series suggests that condition of cod was at a normal level in the 1990s and 2000s. If so, natural mortality associated with cod condition (e.g., due to starvation) would not be expected to be unusually high during this period. It might be argued that interannual variation in condition during the feeding season in September is not a good indicator of condition levels in the spring, when any mortality due to poor condition would be expected to occur. However, in the nGSL stock, the very low condition in May 1994 was associated with poor condition the preceding fall and the following September (Dutil et al. 1995; Lambert and Dutil 1997).

Estimated M of southern Gulf cod 5 years and older increased from about 0.1 in the early to mid 1970s to 0.2-0.3 in the late 1970s to mid 1980s (Swain 2011b). This increase in M might be associated with fisheries-induced declines in age and size at maturation in the 1960s combined with the additional stress of poor fish condition in the late 1970s to mid 1980s (Swain 2011a). If so, mortality due to this cause should have declined in the late 1980s as condition improved.

MULTISPECIES PATTERNS IN THE CONDITION OF MARINE FISHES IN THE SOUTHERN GULF OF ST. LAWRENCE.

Insights into the ecological consequences of the observed patterns in the condition of sGSL cod may be gained by comparing these patterns with those observed for other species in the community. Specifically, we propose two hypotheses for such a comparison. First, if trends in condition are responsible for trends in cod natural mortality (M), then we would expect to see a similar relationship between condition and M for other species having undergone interannual changes in condition of similar magnitude. Second, assuming that condition-related mortality is mainly associated with winter fasting, resulting in critically low condition in spring, we might expect that species with the most pronounced annual changes in condition would also be most vulnerable to increased M .

METHODS

For interspecific comparisons, condition was defined as the predicted intact body weight (i.e., including the weight of all viscera and stomach contents) of individual fishes as a function of length. Because the various components of fish weight (liver, gonads, flesh) have different seasonal and possibly different interannual patterns of change, the trends described here for cod based on total weight may differ from those for the other measures of condition described previously in this document.

All of the data for the analyses were obtained from bottom trawl surveys in the sGSL or the neighboring Sydney Bight area.

Interannual trends in condition

Representative length frequencies and stratified weight measurements have been obtained for all species during all sets in the annual sGSL surveys since 1971 (Hurlbut and Clay 1990). Fish were weighed using spring scales (accuracy $\pm 10g$) from 1971-1989 and with electronic marine

scales (± 1 g for small-bodied species measured on fine scales and ± 5 g for others) since then. Because of these different scales of measurement error, two sets of analyses of interannual changes in condition were undertaken. In the first, only individual weights >20 g and species with a median weight of >20 g were retained to produce time series of condition for the period 1971-2009. The second analysis included all weights and those species that occurred in all years over the period 1990-2009.

Interannual trends in the condition index were obtained from a two-step analysis for each species, s . The first step was used to obtain a residual weight from predicted weight-at-length for the entire series using the following model:

$$1) \quad \ln W_{sijk} = \beta_{0s} + \beta_{1s} G_{sijk} + \beta_{2s} G_{sijk} \cdot \ln L_{sijk} + \beta_{3s} \ln L_{sijk} + \epsilon_{sijk}$$

where $\ln W_{sijk}$ is the \log_e -transformed weight of fish k of species s measured in set j of year i , $\ln L_{sijk}$ is its \log_e -transformed length, and ϵ is the model residual for the fish. The betas are parameters of the equation specific to species s : β_{0s} is the intercept, β_{1s} is a vector of parameters for the class variable gender (G), β_{2s} is a vector of parameters for the interaction between gender and $\ln L$, and β_{3s} is the slope parameter for the effect of $\ln L$. This model (an analysis of covariance) takes into account dimorphic growth in flatfish, skates, white hake and redfish (the effect of gender was not included for the other species). The model was fit using a least-squares approach, with each observation weighted to account for the stratified sampling of weights, the relative abundance of the species in the set and for the proportion of the survey area represented by the set, so as to obtain a true population-level estimate of condition.

The residuals from eqn. 1 were then included in a second model of the form:

$$2) \quad \epsilon_{sijk} = \beta_{4s} + s_{1s}(T_{sji}) + s_{2s}(Y_{si}) + \delta_{sijk}$$

where $s_{1s}(T_{sji})$ is a cubic spline function for species s of the time of day in which set j took place and $s_{2s}(Y_{si})$ is a cubic spline function of year. The effective degrees of freedom for the effect of time of day was set to 2 and those for the year effect were set to five, following some preliminary analyses. The time-of-day effect was included to correct for a potential bias in the analysis owing to the fact that the sGSL survey operated only during the daytime (7:00-19:00) from 1971-1984 and 24 hrs per day thereafter. Diel patterns in weight-at-length (e.g., Fig. 12) are presumably related to fish feeding periodicity and should be independent of effects due to size-dependent differences in diel catchability, for which survey catch rates were adjusted prior to analysis (see Benoit and Swain, 2003). The predicted annual \log_e -residual weight was used as the interannual index of condition.

We tested for density-dependent and temperature-driven changes in condition using multiple regression, for those species for which a condition index was calculated for the full period from 1971-2009. The survey biomass index (mean kg/tow) was used for the density effect for each species except herring, for which biomass from the assessment model was used. The temperature effect was specific to each species and was calculated as the catch-weighted mean temperature occupied in September (Perry and Smith 1994), as described in section 1 for cod.

Seasonal trends in condition

Bottom-trawl surveys of the sGSL and neighboring areas have been conducted in most months and were used to characterize the seasonal changes in condition in sGSL fish species. These surveys include seasonal surveys undertaken in 1986-1987 in the southeastern Gulf of St. Lawrence, 1985-1988 in St. Georges Bay and 1989-1992 in the southwestern Gulf, as well as January surveys conducted annually from 1994-1997 in the Cabot Strait (Clay, 1991; Benoit et al., 2003; Darbyson and Benoit, 2003; DFO unpublished data). A two-step approach was used to produce seasonal trends in condition for each species. In the first step, a residual weight-at-length (ϵ_{sijk}) was calculated as:

$$3) \quad \epsilon_{sijk} = \ln W_{sijk} - (\beta_{0si} + \beta_{1si} G_{sijk} + \beta_{2si} G_{sijk} \cdot \ln L_{sijk} + \beta_{3si} \ln L_{sijk})$$

where $\ln W_{sijk}$ is the log_e-transformed weight of fish k , of species s , in year i , in set j , $\ln L_{sijk}$ is the log_e-transformed measured length, G is the class variable gender, and β_{0si} , β_{1si} , β_{2si} , and β_{3si} are parameters for the length-weight analysis of covariance fit to observations made in September of year i during the annual September survey. Eqn. 3 accounts for interannual changes in condition by calculating the condition index relative to the estimated September length-weight relationships for the same year as the seasonal survey was conducted.

The ϵ_{sijk} from eqn. 3 were then used in the following model:

$$4) \quad \epsilon_{sijk} = \beta_{5s} + s_{1s}(T_{sij}) + s_{3s}(D_{sij}) + \delta_{sijk}$$

where $s_{1s}(T_{sij})$ is again a cubic spline function for species s of the time of day in which set j in year i took place and $s_{3s}(D_{sij})$ is a cubic spline function of the calendar day for set j . The effective degrees of freedom for the effect of time of day was set to 2 and those for the calendar day effect were set to four, following some preliminary analyses. The predicted annual log_e-residual weight from eqn. 4 was used as the seasonal index of condition.

RESULTS AND DISCUSSION

Interannual trends in condition

An interannual index of condition covering the period 1971-2009 was produced for 12 sGSL marine fish species (Fig. 13). For most species, including cod, the difference in predicted body weight between the periods of lowest and highest condition was 6-10%. For a number of species, condition was highest in 1971, declined to its lowest levels sometime during the late 1970s or early 1980s, subsequently increasing and then fluctuating about more intermediate levels. This trend was shared by species that have declined considerably in abundance, possibly due to high M , such as cod, thorny skate and American plaice, as well as species with stable abundance such as longhorn sculpin and yellowtail flounder.

The trend in the condition for cod was strongly related to the biomass index, indicating an important density-dependent effect (Table 1; Fig. 14). Density-dependent effects were also found for redfish, plaice and herring, and a positive effect of density was found for witch flounder. Statistically-significant negative effects of abundance-weighted temperature were found for winter flounder, thorny skate and eelpouts. The effect for cod approached significance at the 0.05 level and was positive.

An interannual index of condition covering the period 1990-2009 was produced for 29 sGSL marine fish species (Fig. 15). There was a dominant pattern in condition for almost the entire marine fish community over this period: relatively high condition at the beginning of the series, a drop to relatively low levels during the mid to late-1990s, followed by increases to intermediate or high levels. This suggests a common environmental effect experienced by members of the community. This trend in condition is shared by species for which abundance has declined or remained stable since 1990 (Fig. 15). Condition for species that have increased in abundance since 1990 has improved since the late 1990s low, but has not recovered as strongly as observed in other species. This may reflect a density-dependent effect.

For Atlantic cod, the patterns observed here are consistent with those observed in the seasonal condition monitoring program, which covered the same time period. Data collected by that program indicate that, in contrast to the patterns observed in the spring, condition in the fall was highest in the early 1990s, declined to a lower level in the late 1990s and early 2000s, and then recovered (Fig. 4). However, for Atlantic cod and some other species, in particular American plaice and yellowtail flounder, the changes in condition observed in the 1990-2009 period are relatively small compared to the changes observed earlier in late 1970s and early to mid 1980s (Fig. 13).

Overall there does not appear to be a common relationship among species between apparent high adult mortality and the trends and amplitude in interannual changes in condition. Density-dependence and changes in the environment both appear to contribute to changes in condition. For species for which trends in M have been estimated (cod, white hake, and thorny skate), periods of low condition largely predate the years of most rapid increase in M (Benoit et al. 2010; Swain 2011a,b).

Seasonal trends in condition

Seasonal trends in condition were estimated for 15 sGSL fish species (Fig. 16). For most species, condition was lowest during winter, increasing gradually to a peak during the summer, followed by a relatively rapid decline in the autumn. However, the amplitude of the seasonal cycle differed among species; e.g., the predicted weight-at-length of winter flounder, winter skate, yellowtail flounder and longhorn sculpin varies considerably less seasonally compared to the other species. Apparent trends in M appear to be unrelated among species to the annual magnitude of condition change (high amplitude, high M : e.g., cod, thorny skate, white hake; low amplitude, high M : e.g., winter skate, winter flounder; high amplitude, apparently low M : herring, Greenland halibut; low amplitude, apparently low M : longhorn sculpin).

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Table 1. Results of species-specific regression analyses of the predicted annual residual weight as a function of biomass and abundance-weighted mean temperature.

species	Effect of biomass			Effect of temperature		
	Estimate	SE	P-value	Estimate	SE	P-value
Atlantic cod	-0.0002	0.0000	<0.0001	0.0026	0.0013	0.0574
White hake	-0.0013	0.0009	0.1826	0.0016	0.0015	0.2852
Redfish	-0.0010	0.0003	0.0058	0.0039	0.0068	0.5739
American plaice	-0.0003	0.0001	0.0153	-0.0011	0.0053	0.8400
Witch flounder	0.0121	0.0049	0.0183	0.0011	0.0022	0.6224
Yellowtail flounder	-0.0048	0.0031	0.1324	-0.0025	0.0013	0.0717
Winter flounder	-0.0001	0.0003	0.7654	-0.0025	0.0011	0.0348
Herring ¹	-3.57E-7	0.90E-7	0.0004	0.0028	0.0036	0.4339
Thorny skate	-0.0069	0.0036	0.0686	-0.0133	0.0037	0.0011
Longhorn sculpin	0.0096	0.0074	0.2055	-0.0003	0.0013	0.7942
Sea raven	0.0254	0.0140	0.0793	0.0024	0.0021	0.2533
Eelpouts	0.0040	0.0061	0.5145	-0.0233	0.0070	0.0022

¹The biomass estimated from sequential population analysis was used instead of the survey biomass index

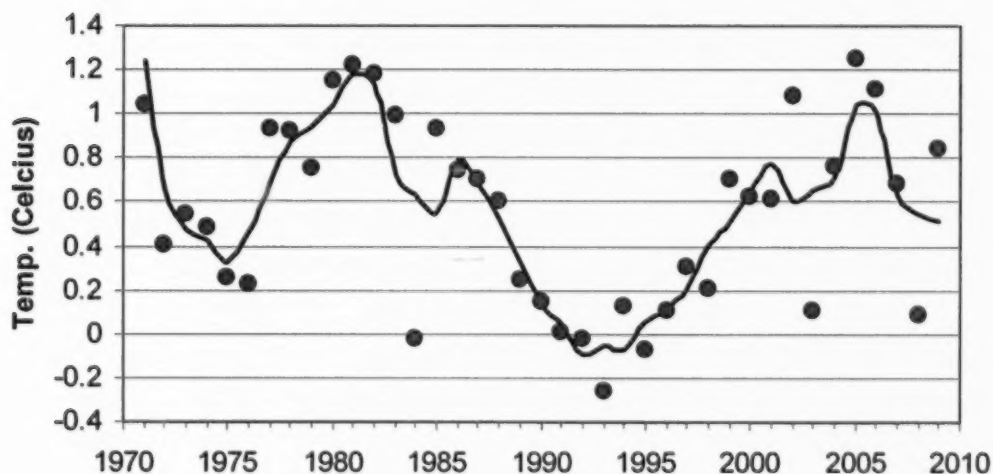


Figure 1. Index of Cold Intermediate Layer temperature in the southern Gulf of St. Lawrence. Circles are the mean temperature in the 60-120 m water layer in September. Line is a loess smooth to the data.

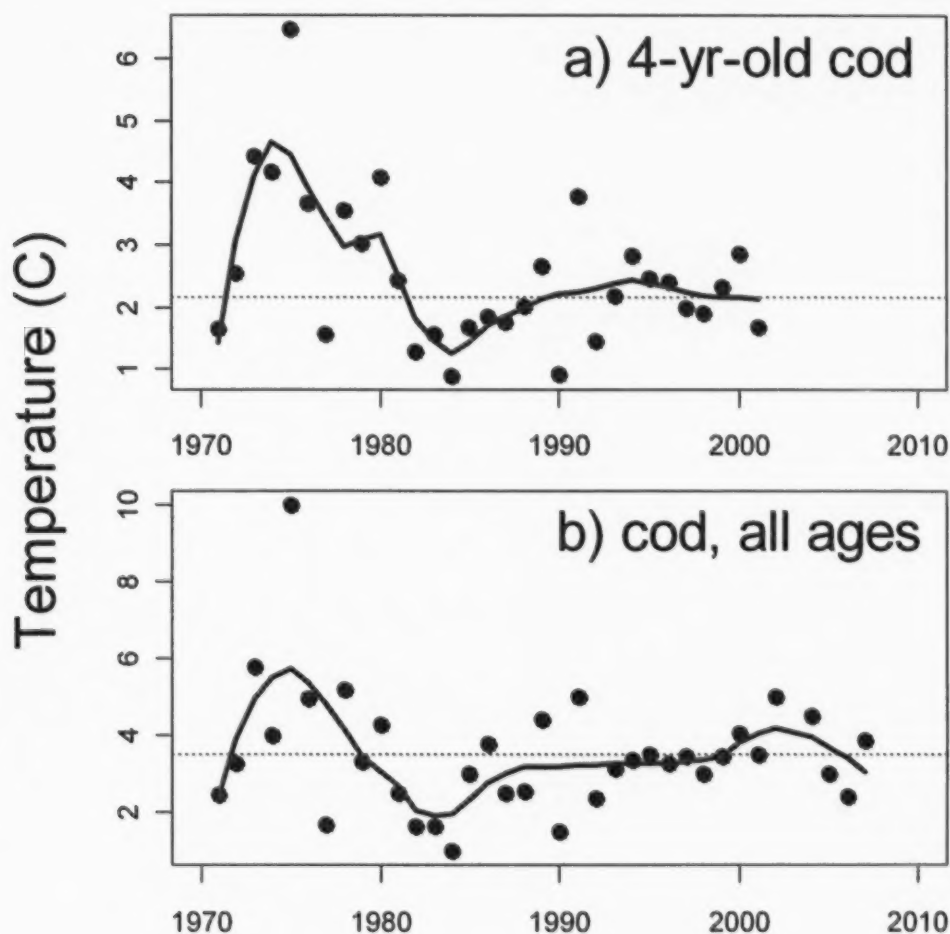


Figure 2. Ambient temperature of southern Gulf cod in September. Ambient temperature is the average temperature occupied by cod based on catches in the September survey. Results in panel b are based on q-corrected survey catches (i.e., results in this panel are most heavily influenced by the distribution of small cod). The solid line is a loess smooth to the data. The dotted line is the long-term mean.

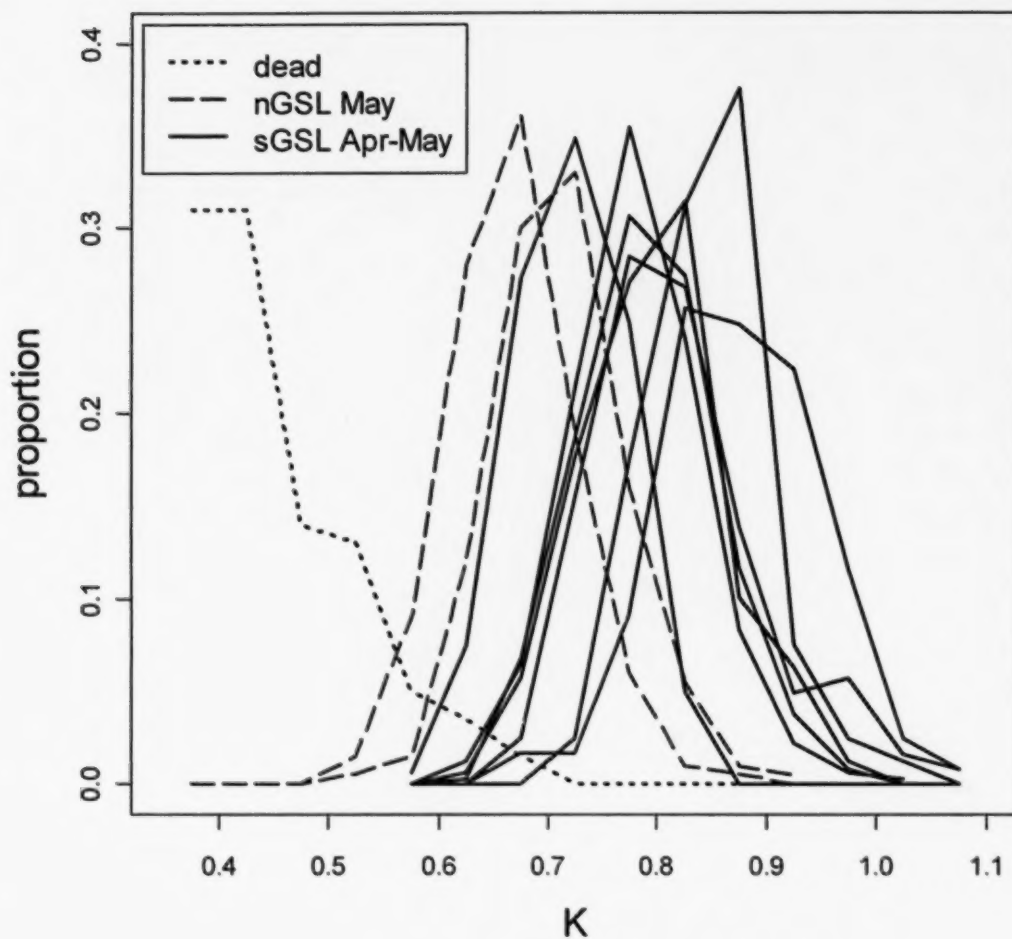


Figure 3. Distribution of condition factor K in dead or moribund fish from starvation experiments in the laboratory (dotted black line, from Lambert and Dutil 1997), in wild fish collected from the northern Gulf in May 1994 and 1995 (dashed red lines, from Lambert and Dutil 1997), and in wild fish collected from the southern Gulf in late April or early May 1992-2010 (solid blue lines).

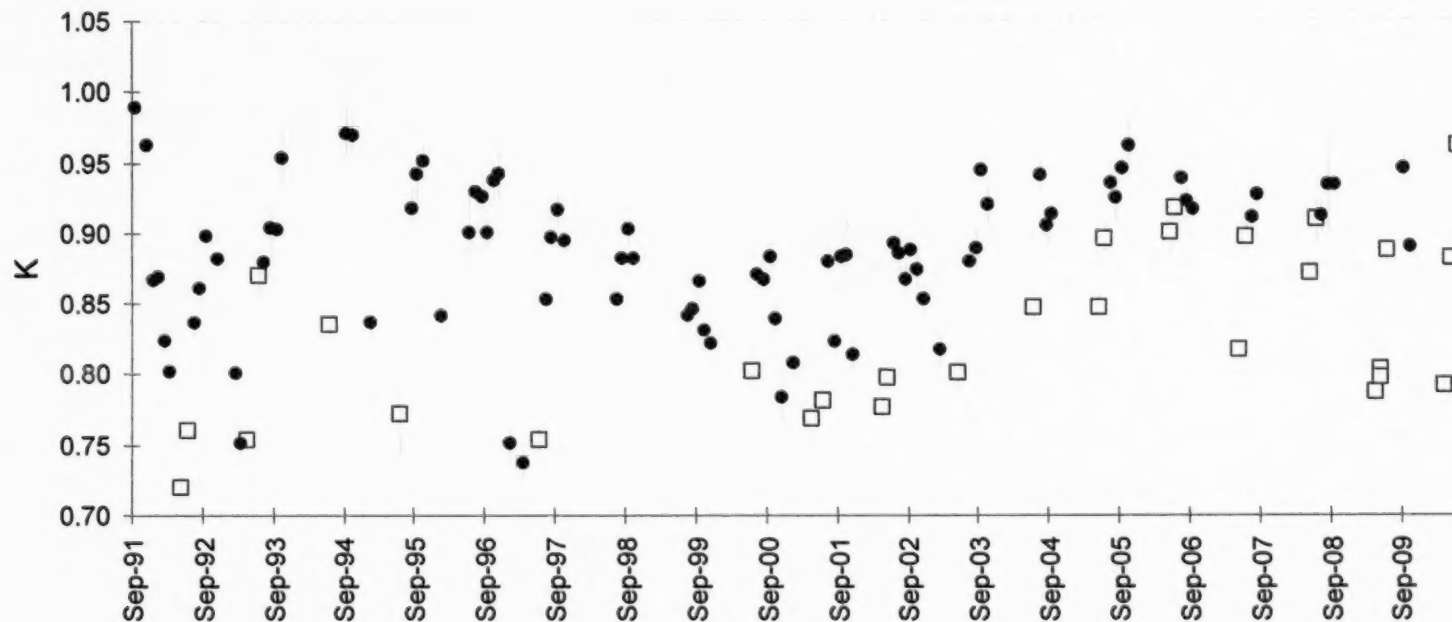


Figure 4. Seasonal and interannual variation in condition factor (K) of southern Gulf of St. Lawrence cod. Vertical lines are 95% confidence intervals. Squares indicated samples collected in April, May or June.

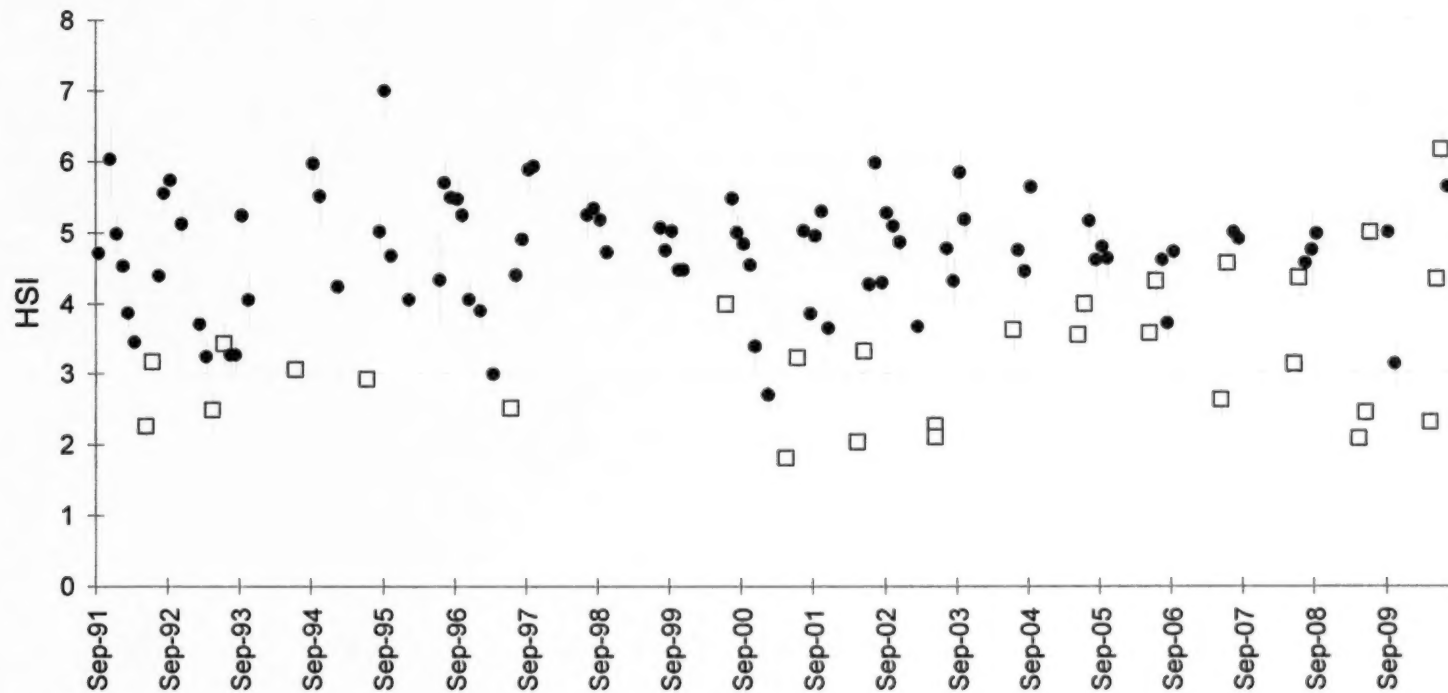


Figure 5. Seasonal and interannual variation in hepatosomatic index (HSI) of southern Gulf of St. Lawrence cod. Vertical lines are 95% confidence intervals. Squares indicated samples collected in April, May or June.

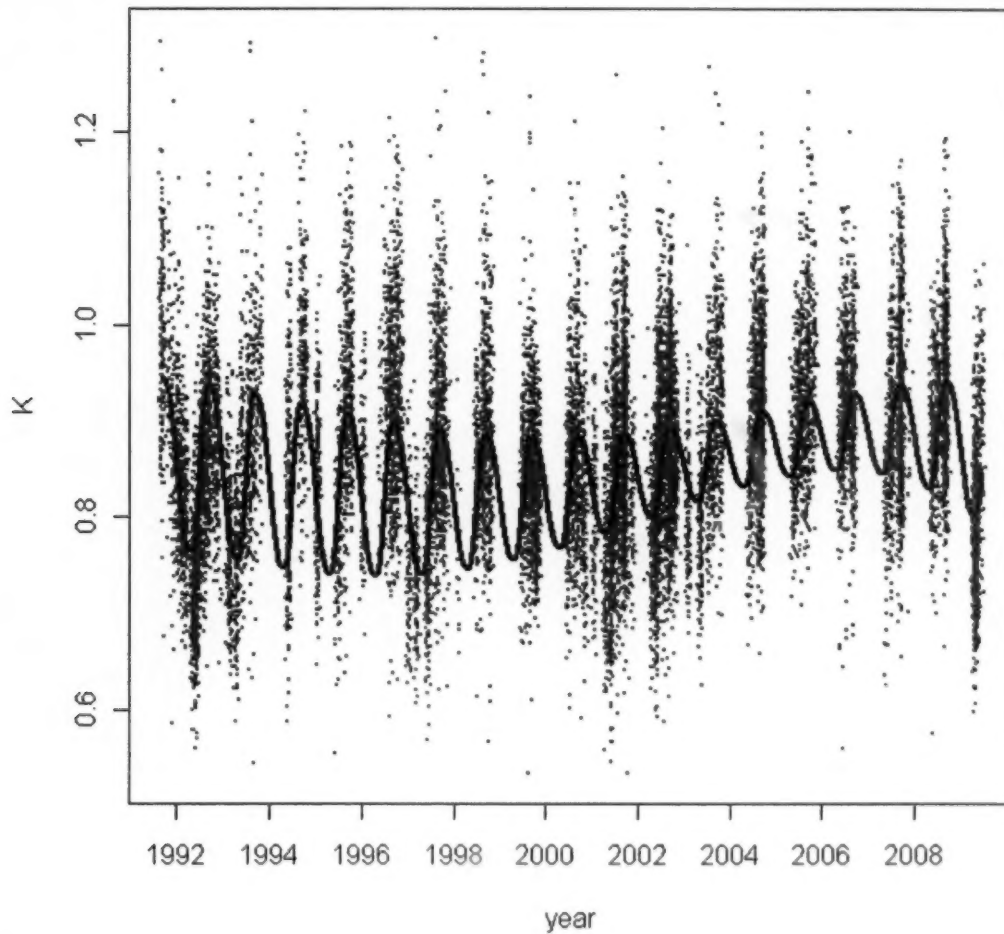


Figure 6. A spline model with seasonal and interannual components (line) fitted to the observed cod condition (K) values. A small random variation was added about the x observations in order to facilitate the visualization of the distribution of the observations. Only data up to June 2009 were available for this analysis.

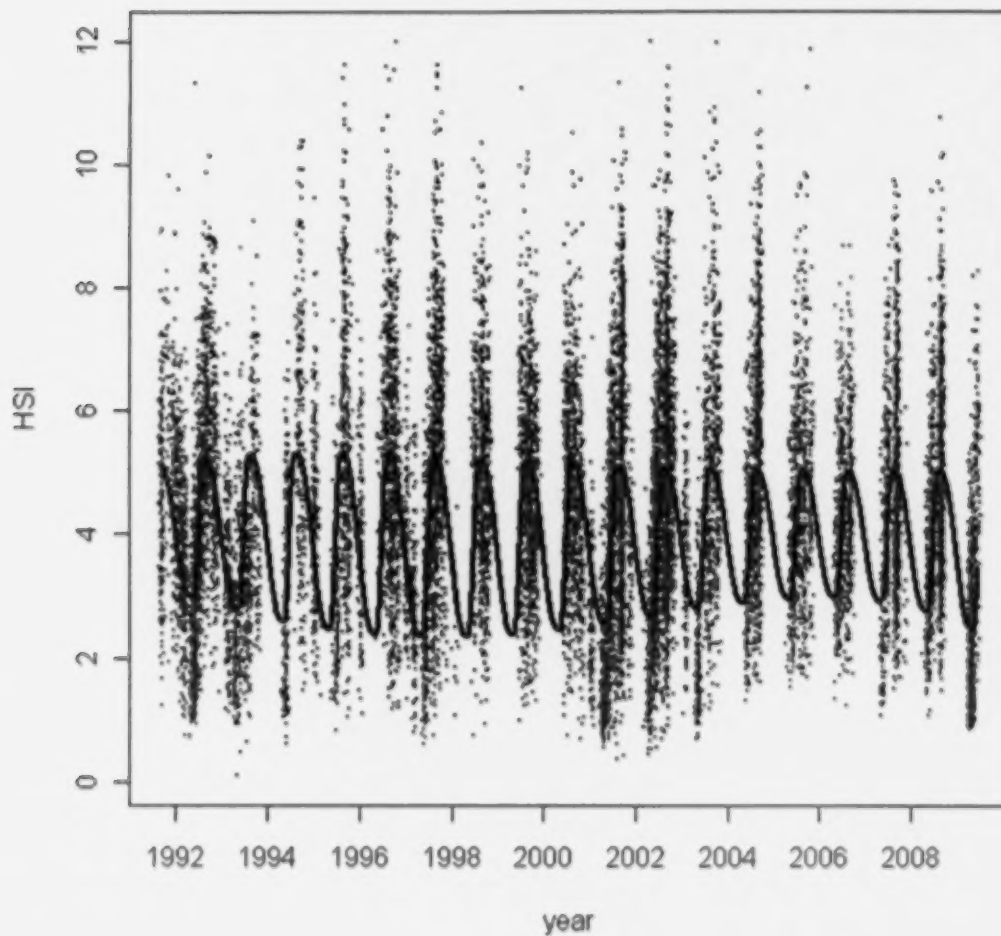


Figure 7. A spline model with seasonal and interannual components (line) fitted to the observed hepatosomatic index (HSI) of cod. A small random variation was added about the x observations in order to facilitate the visualization of the distribution of the observations. Only data up to June 2009 were available for this analysis.

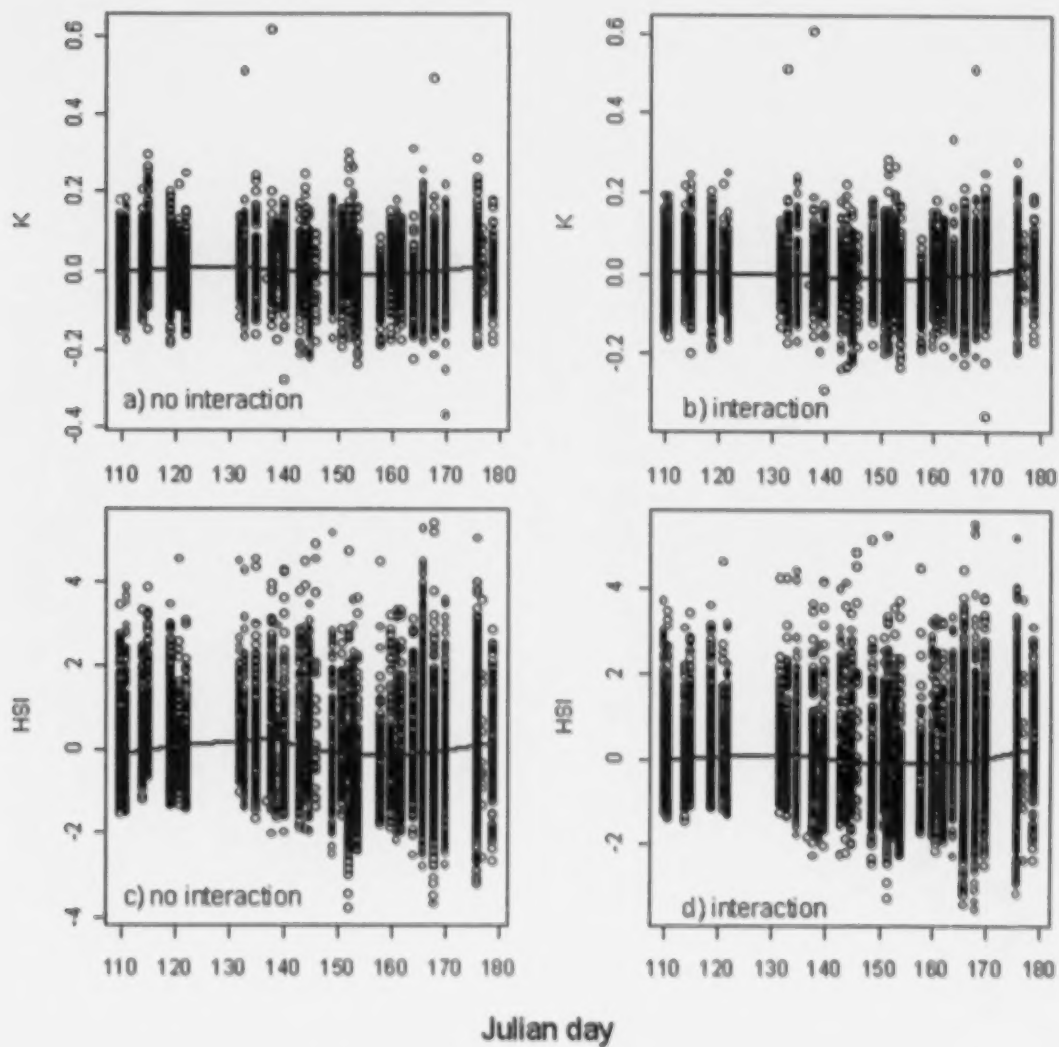


Figure 8. Residual plots for models relating indices of cod condition (K or HSI) in April-June to year and Julian day.

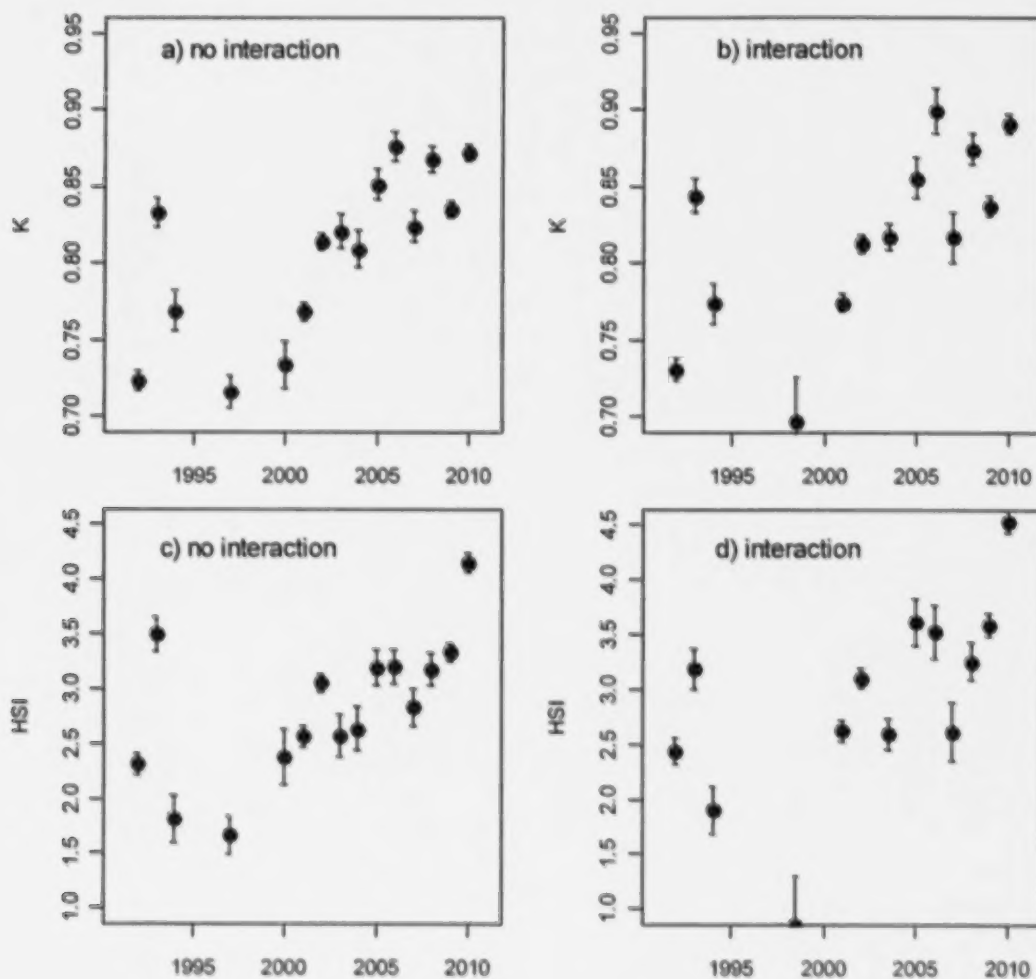


Figure 9. Predicted K (panels a and b) and HSI (panels c and d) of southern Gulf cod on May 23 (the mean date in the April-June data). Predictions are from a model relating condition in spring (April-June) to year and Julian day, assuming homogeneous (a,c) or heterogeneous slopes (b,d) for the covariate Julian day.

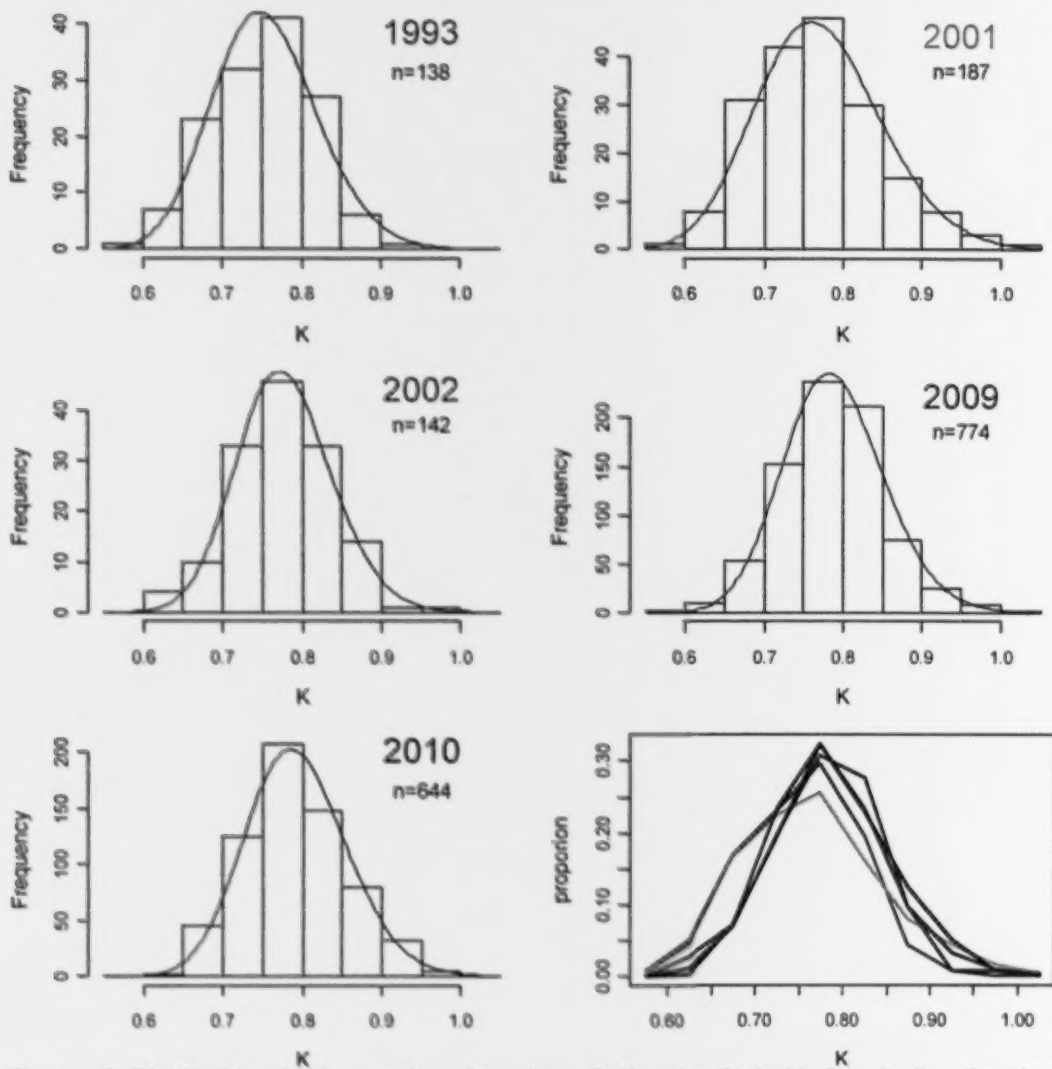


Figure 10. Distribution of K in samples of southern Gulf cod collected in late April or the start of May (April 30 – May 03 in 2009). Lines in the bottom right panel are colour-coded to match the colour of the year label in the other panels. Lines in these other panels show a lognormal distribution with the same mean and SD as the data.

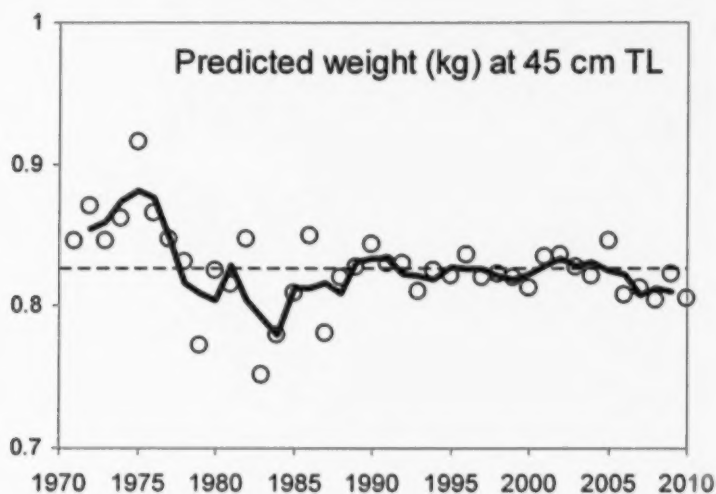


Figure 11. Longterm index of condition of southern Gulf cod. The index is the predicted weight at a length of 45 cm, based on the parameters of the annual length-weight relationship. The blue line is a running 3-yr average and the dashed line is the 1971-2010 mean.

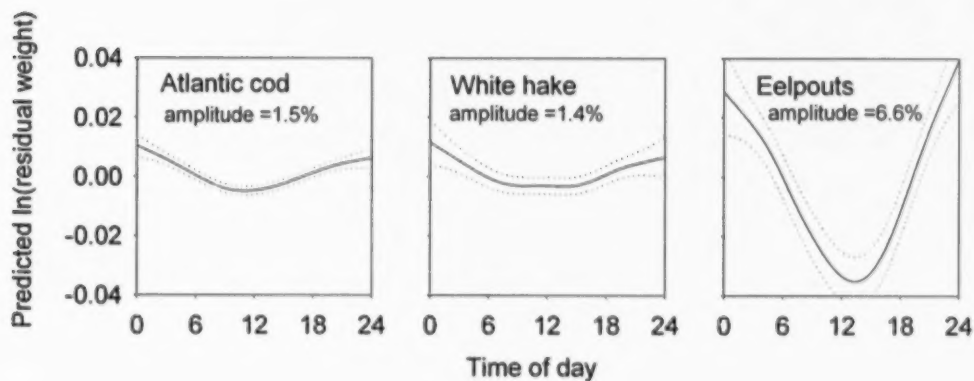


Figure 12. Predicted \log_e -residual weight as a function of time of day for Atlantic cod, white hake and eelpouts captured in the sGSL September survey 1971-2009. The overall percentage body weight change over the diel cycle is indicated in the panel for each species.

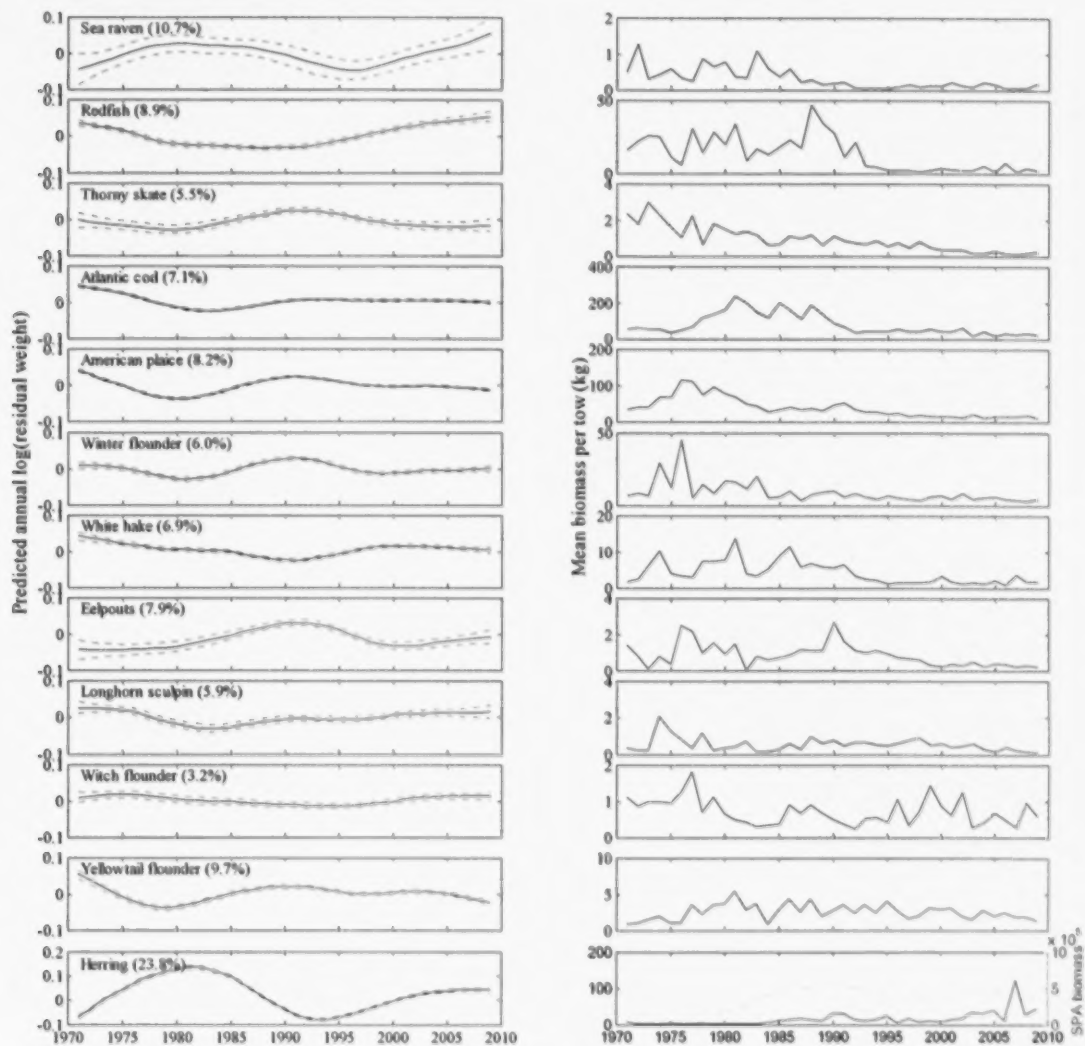


Figure 13. Interannual patterns in the index of condition (predicted annual \log_e -residual weight \pm 95% C.I.; left column) and biomass index (right column) for the 12 marine fish species for which there were sufficient reliable condition data prior to 1990. Note that for the plots of the condition index, all species except herring share a common y-axis scale. The number indicated in each panel is the percentage change in body weight between the periods of lowest and highest observed condition.

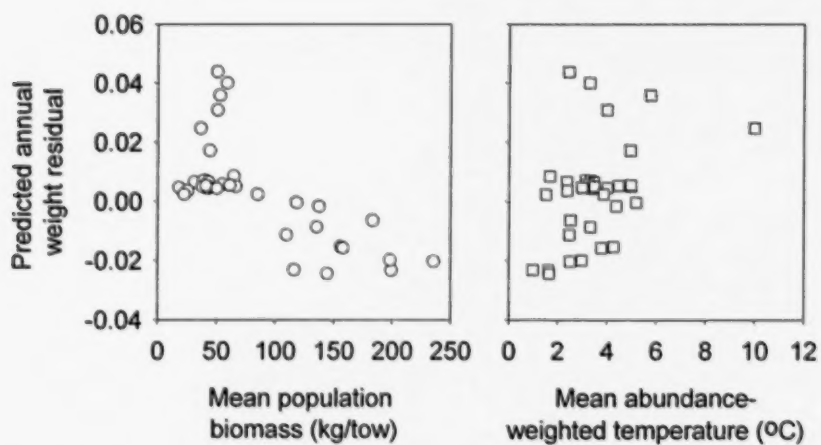


Figure 14. Predicted annual \log_e -residual weight of Atlantic cod in the sGSL September survey as a function the mean population biomass (left) or abundance-weighted mean occupied temperature (right).

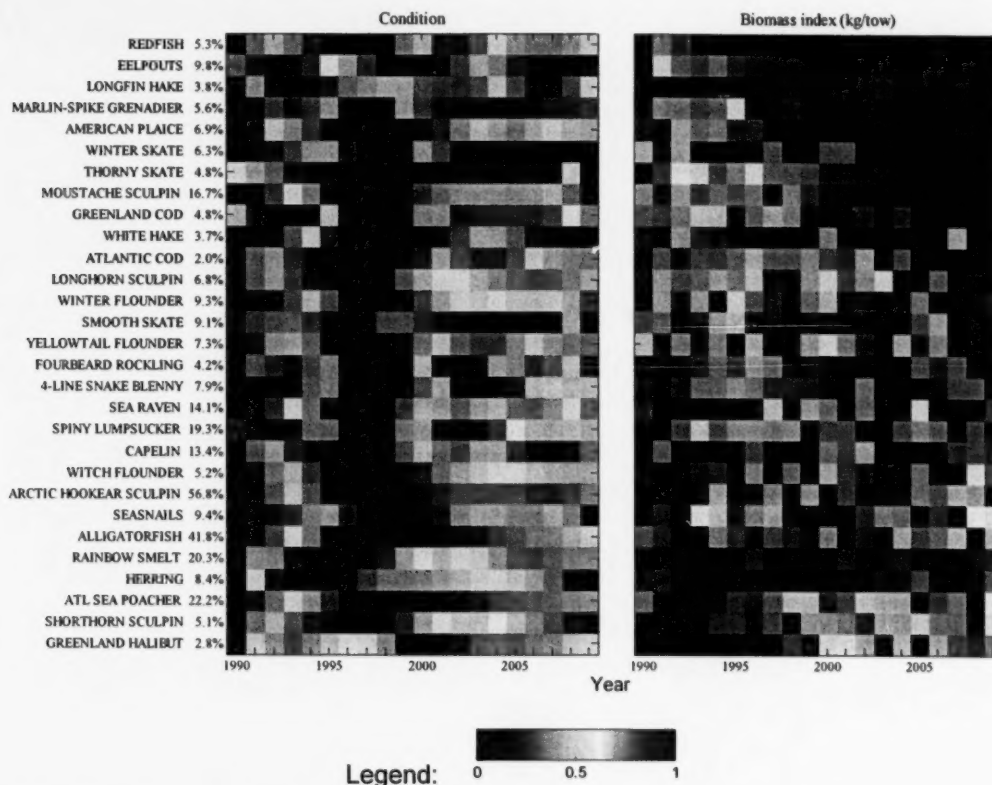


Figure 15. Time series of the standardized condition index (left) and biomass index (right) for 29 fish species in the sGSL annual survey, 1990-2009. Dark red indicates relatively high condition or biomass, whereas dark blue indicates relatively low levels. The numbers next to the species names are the percentage change in predicted body weight between the periods of lowest and highest observed condition. Note that because this analysis includes fish <20g and because the spline for the effect of year was unconstrained by patterns in condition prior to 1990, the percentage change calculated for 1990-2009 may exceed that calculated for 1971-2009 for Fig. 3. Note also that higher values for the percentage changes in predicted weight for smaller-bodied species such as alligatorfish, hookear sculpins, poachers and lumpsuckers likely reflect higher overall measurement errors for these species.

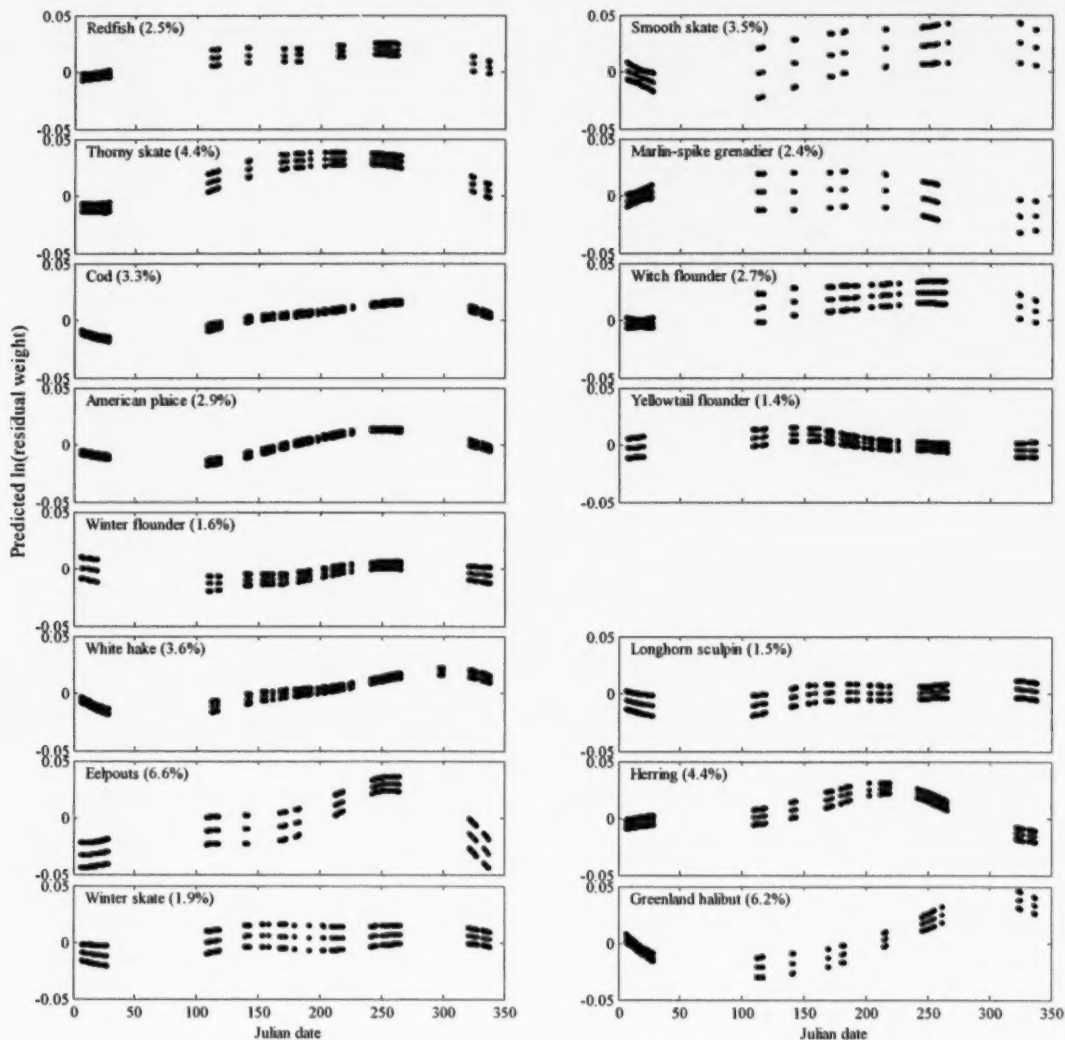


Figure 16. Annual pattern in the condition index (predicted annual \log_e -residual weight in red \pm 95% CI in black) of fifteen marine fish species in the sGSL, based on seasonal surveys. Points are plotted only for those calendar days for which data were available. The number indicated in each panel is the percentage change in body weight over the seasonal cycle. Species have been sorted (top to bottom, left to right) approximately in the same manner as in Figure 13. Panels for the three species for which adult natural mortality presently does not appear to be elevated (longhorn sculpin, herring and Greenland halibut) are grouped separately at the bottom right of the figure.